SPECIES RICHNESS AND FLORISTIC COMPOSITION OF CHOCO REGION PLANT COMMUNITIES

by
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The Chocó phytogeographical region of coastal Colombia and adjacent Ecuador is well known as a region of unusually high endemism in plants (GENTRY, 1982a, 1986b), birds (TERBORGH & WINTER, 1982), and butterflies (BROWN, 1975, 1982). The region is also reputed to be unusually diverse biologically (GENTRY, 1978, 1982a) but much of the data base for this assumption is rather anecdotal and for birds and heliconiinae butterflies (probably the best known groups of organisms) it is clear that faunistic community diversity of the coastal Chocó is substantially less than in much of upper Amazonia (J. TERBORGH, pers. comm., K. BROWN, pers. comm.).

The only community level datum available for plants from coastal Colombia is the incompletely analyzed 1000 m^2 sample of all plants over 2.5 cm dbh. from near Tutunendó, included in GENTRY's (1982b) overview of neotropical diversity patterns. GENTRY's Chocó sample had the highest number of species of a series of similar sample sites and he concluded that community level plant species richness increases directly with precipitation. Many additional 1000 m^2 samples are now available, both from the Chocó region and from species rich forests of upper Amazonia and many other parts of the world (GENTRY, 1982b, 1985, original data). It is the purpose of this paper to compare the Chocó region data sets with similar samples from surrounding areas and describe some of the unusual features that seem to characterize Chocó forests.

SITES AND METHODS

All samples were made with the technique described by Gentry (1982b). Each sample consists of ten 2 x 50 m transects in which all plants $\geq$ 2.5 cm dbh. (2.5 cm greatest diameter for lianas) which are rooted in the sample

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area are censused. In each sample the individual transects are laid out in a predetermined direction (typically perpendicular to a trail) from a haphazardly selected starting point. Adjacent transects are generally separated by 20 m or more except that subsequent lines were sometimes continued from the end point of a preceeding line. In several Peruvian and one Venezuelan site the 2 x 50 m transects constituted one meter on either side of the subplot limits of 1 ha. tree plots.

Data collected by this technique are now available from 71 sites in 23 countries on six continents as well as several islands. Included in the data set are two sites in the wet Pacific coast forests of Colombia (Bajo Calima, Tutunendó) and three samples from coastal Ecuadorian wet forest [río Palenque (2), Centinela].

The two lowland Pacific coast forest sites in Colombia are both in the strip of excessively high rainfall along the río Atrato and río San Juan that makes the Chocó the wettest region in the world (GENTRY, 1982a; Sota, 1972). The Tutunendó site (5° 46' N, 76° 35' W) is on the Quibdó-Tutunendó road, 14 km E of Quibdó ca. halfway between Quibdó and Tutunendó, in Chocó Department. Annual precipitation at Quibdó is 8558 mm and at Tutunendó, perhaps the rainiest place in the world, 11770 mm (Sota, 1972; GENTRY, 1982a); at the study site annual precipitation is probably between 9000 and 10000 mm. The altitude of the study site is about 90 m. The soil is of the typical reddish lateritic type, rich in aluminum and iron and low in silica. Although far from rich, the soil has substantially more of such potentially critical nutrients as potassium (65 ppm), phosphorus (4.3 ppm) and nitrogen (4940 ppm) than does that at Bajo Calima (STARK & GENTRY, in prep.). The sample was made in two installments, in January 1979 and January 1981. Selective cutting in an otherwise apparently undisturbed forest was beginning at the time the study was being conducted; subsequently the forest has been greatly altered. The closed canopy of the original forest of the study area is 30-40 m tall with prevalent epiphytes, especially hemiepiphytic vines, and a thick covering of moss on most trunks and branches.

The Bajo Calima site is in Valle Department north of Buenaventura (3° 55' N, 77° 0' W) not far from the Pacific coast. Annual precipitation at the nearby Pulpapel Station is 7470 mm. The altitude of the study area was about 100 m. The soil is an unusual white clay with no measurable phosphorus or boron as well as the lowest zinc content of any of a broad series of neotropical soil types (STARK & GENTRY, in prep.). The sample was conducted in three installments: December 1981, February 1983, and July 1984. The Bajo Calima area is in the Cartón de Colombia concession area and sampling was carried out ca. 0.5-1 km beyond the end of the access road to forest parcels

being clear cut for paper pulp by that company. The study area had recently been surveyed for future cutting and a few of the largest timber trees felled and removed by freelance loggers who preceed the clear-cutting operation. The branches of the recently felled commercial timber trees still retained dried leaves, and in the only case where one of their stumps entered the sample, it was identified and scored as a live tree. The first nine subsamples were made in the same patch of forest (Juanchaco Palmeras) but that patch had been clear cut when the final subplot was sampled in 1984, and a nearby patch of physiognomically and floristically similar forest was sampled instead. The closed canopy of the undisturbed forest of this area is around 30 m high with many trees marked by a pronounced tendency to small crowns and sclerophyllous leaves.

The two sites for which 0.1 ha. data sets are available in the Ecuadorian part of the Chocó region are Centinela and río Palenque. The río Palenque Science Center, the last patch of the coastal lowland wet forest that formerly formed a narrow band extending south along much of the western base of the Ecuadorian Andes, has been extensively studied (e. g., DODSON & GENTRY, 1978) and is floristically the best known part of the Chocó region. About 100 of the 1100 plant species now known from río Palenque were discovered and described during the process of writing a local florula. The forested area of río Palenque in which two 0.1 ha. samples were made is less than 1 km in total extent. The altitude of the field station is between 150 and 220 m, annual rainfall is about 2980 mm, and the rich soil is recent alluvium. For additional site description, see DODSON & GENTRY, (1978).

The Centinela 0.1 ha. sample was made in 1984 in the last patch of forest along a 500-600 m altitude ridge line about 8 km E of the río Palenque Science Center. This ridge, with a rich soil similar to that at río Palenque, is separated from the main Andean Cordillera by a flat 15 km broad valley with an altitude of about 300 m. Centinela is characterized by a pronounced cloud forest effect and extreme local endemism (GENTRY, 1986b; DODSON & GENTRY, in prep.). The adjacent valleys and lower slopes of the ridge had been deforested prior to the 1000 m^2 sample and the rest of the ridge top has since been clear-cut as well (see GENTRY, 1986b). Rainfall at Centinela is unknown but may be similar to the 3000 mm at Santo Domingo de los Colorados farther north at the same altitude.

PHYSIOGNOMY

The structure of lowland neotropical forests as measured by this technique tends to be remarkably constant (GENTRY, 1982b; EMMONS and GENTRY, 1983). Number of trees $\geq$ 10 cm dbh. per 0.1 ha. in sampled neotropical moist

and wet lowland forests averages 64 (38 to 93) and number of lianas $\geq$ 2.5 cm diameter averages 68 (31-123) (Table 1). Altogether neotropical moist and wet forests average 375 (286-514) plants $\geq$ 2.5 cm in diameter in 0.1 ha. Neotropical moist and wet lowland forests are also characterized physiognomically by the prevalence of palms, averaging about 30 palm stems $\geq$ 2.5 cm in diameter and 8 stems $\geq$ 10 cm diameter per 0.1 ha. (EMMONS & GENTRY, 1983). In contrast, there are a number of fundamental physiognomic differences between neotropical and paleotropical forests. For example, paleotropical forests have many fewer canopy palms. Neotropical forests have fewer lianas than African ones and more than Asian ones (EMMONS & GENTRY, 1983).

The Chocó region pluvial forest sites (Table 2) are structurally unique in several ways. They have significantly higher densities than other moist and wet forest sites. The Tutunendó sample includes more individual plants than does any other continental site in the world. The Bajo Calima sample has the fourth highest density of any continental site, being exceeded only by the Tutunendó one, a Peruvian tahuampa forest where a virtual thicket of *Sorocea* treelets dominates the understory, and an Asian dipterocarp forest site at Semengoh, Sarawak. In their high stem densities the Chocó forests are structurally similar to the typical forests of subtropical islands in the hurricane belt (e. g. Mauritius, New Caledonia).

Although the two Chocó pluvial forests have exactly the same average number of sampled climbers (68) as do the moist and wet forest sites, half of their climbers are hemiepiphytic. Other lowland forests rarely have more than one or two sampled hemiepiphytes. Both lowland coastal Ecuadorian wet forests shared with the Chocó pluvial forests the prevalence of hemiepiphytic climbers. Fourteen of the 70 sampled climbers at Centinela were hemiepiphytic and 15-22 of the 45-63 sampled chimbers in replicate río Palenque samples were hemiepiphytic. No other site had more than 7 sampled hemiepiphytes.

The Chocó pluvial forests also have more trees $\geq$ 10 cm dbh. than do other lowland neotropical forests. The Bajo Calima site has the greatest density of trees $\geq$ 10 cm dbh. of any continental neotropical sample site while the Tutunendó one is fourth in this regard. Interestingly one of the sites from Ecuadorian Chocó (Centinela) has the second highest density of all for trees $\geq$ 10 cm dbh. while the other one (río Palenque) has the second lowest density of large trees. The Centinela site, a 500-600 m ridge top, has a marked cloud forest effect that may account for its high tree density. High density of trees $\geq$ 10 cm dbh. is typically associated with reduced numbers of large emergents and seems to be a characteristic feature of both hurricane-belt and poor-soil forests.

We may conclude that Chocó forests in general, even in relatively dry areas like río Palenque (2980 mm of precipitation per year), seem to be characterized by replacement of freeclimbing lianas by hemiepiphytic ones. At least in the case of the pluvial forests, the Chocó area also seems to be physiognomically characterized by unusually high densities of trees $\geq$ 10 cm dbh. and uniquely high overall stem densities.

DIVERSITY

The lowland pluvial forests of the Colombian Chocó are the most species rich plant communities in the world (compare Table 2 with Tables 1 and 3 and with GENTRY, 1985). The two pluvial forest samples average 262 species $\geq$ 2.5 cm in diameter in 0.1 ha. This compares with an average of 151 species for equivalent 0.1 ha. samples from 22 lowland neotropical moist and wet forest sites. The most diverse neotropical samples from outside the Chocó region are from the wet aseasonal forests near Iquitos in Amazonian Perú [Mishana (249 species); Yanamono (230 and 212 species in replicated samples)]. No other Neotropical sample has as many as 200 species $\geq$ 2.5 cm diameter in a 0.1 ha. sample.

While the two Chocó area pluvial forests are the world's richest as measured by these 0.1 ha. samples, some Southeast Asian forests are almost as rich. The richest paleotropical sample, from dipterocarp forest at Semengoh Forest Reserve near Kuching, Sarawak, has over 243 (and possibly as many as 250) species. It is noteworthy that the diverse Chocó area forests, like the most species rich Southeast Asian one, have unusually high stem densities. Thus part of the high species richness for 0.1 ha. samples is due to the greater number of individuals included in these samples. If species per individual rather than species per unit area were taken as a diversity index, some of their phenomenally high diversity would be lost. Nevertheless, the Chocó samples would remain as diverse as any in the world.

In view of the strong correlation between neotropical plant species richness and precipitation (GENTRY, 1982b), it is not surprising that the Chocó samples, from the wettest part of the Neotropics, have the most plant species. However, the additional samples now available show that the near-linear increase in species richness with precipitation suggested by GENTRY (1982b) obtains only for annual rainfalls between 1500 mm and 4000 mm. Even though the two pluvial forest samples have more plant species than any from upper Amazonia, their difference in diversity from the Iquitos area values is not pronounced, despite a doubling of the annual precipitation (Figure 1). Apparently the richness of neotropical plant species communities approaches an asymptote near 4000 mm of annual precipitation. Such an asymptote is strongly

suggestive that plant communities in high rainfall areas like the Chocó may have reached saturation and achieved an ecological equilibrium (GENTRY, 1985).

The Chocó area forests are unusually species rich both in trees and climbers. However, as noted above, a high proportion of their climbers are hemiepiphytic so that relatively few species of free-climbing lianas are included in the Chocó samples. While the two Chocó samples have by far the greatest tree species diversity of any 0.1 ha. neotropical sample, a disproportionate part of the tree species are represented only by small diameter individuals. If only trees $\geq$ 10 cm dbh. are considered, the diversity of the Chocó sites is equalled or exceeded by a number of sites in Amazonian Perú (all three Mishana samples, Yanamono, Cocha Cashu) (Table 1).

While the 1000 m^2 samples emphasized here measure only trees, large shrubs, and thick-stemmed lianas, other habit groups also make important contributions to the overall plant community diversity of the wet Chocó area forests. Epiphytes, small shrubs, and terrestrial herbs are all richly represented in these forests. Sampling of these habit groups is exceedingly difficult and has been attempted in only a few tropical forests in the entire world (GENTRY & DODSON, 1986). Data from the río Palenque Biological Center, near the southernmost extreme of the Chocó phytogeographical area, indicate the importance of other habit groups. Almost one fourth (22%) of all the plant species at río Palenque are epiphytes. In a 1000 m^2 sample of the río Palenque forest where all vascular plants were censused, 35% of the 365 species and 63% of all the individual plants censused were epiphytic. Terrestrial herbs constitute 14% of the species and shrubs 11% in this same sample, whereas trees and free-climbing woody lianas together constitute only 34% of the species and less than 10% of the individuals, even though juveniles were included in the sample (GENTRY and DODSON, 1986). Such counts demand a level of knowledge of the flora far beyond current capabilities in the Colombian Chocó. Nevertheless we may assume that epiphytes and terrestrial herbs will prove to contribute at least as much to the plant species diversity of the Chocó region pluvial forests as they do to río Palenque.

Actual census data are available for one additional habit component of several Chocó area forests. Levels of flowering and fruiting were sampled at 13 different Neotropical sites along a 500 m transect and within 2½ m on either side of a trail and 5 m of the ground (GENTRY & EMMONS, 1986). In 55 replicate samples, a strong correlation was found between level of understory fertility, soil type, and strength of the dry season: Areas with weak (or no) dry seasons and intermediate to rich soils consistently have about 64 fertile plant species and 174 individuals in such a sample at any given time, those with very poor soil and a strong dry season average only 5 fertile species and 8 fertile individuals, and those with either strong dry seasons and

good soils or weak dry seasons and very poor soils have intermediate values. Included in this data set are samples from Mecana, north of Bahía Solano near the coast of Chocó Department, from Bajo Calima (3 replicates), and from río Palenque, Ecuador (3 replicates). All of these Chocó area wet and pluvial forests, including the one at Bajo Calima on white clay, have the high levels of understory fertility that we interpret to be associated with high productivity sites. The high levels of flowering and fruiting in the understory of the trans-Andean Chocó forests are similar to those in good-soil, weak-dry-season upper Amazonian forests.

FLORISTIC COMPOSITION

Ecological analyses in the Chocó region are greatly complicated by the inadequacy of the taxonomic data base. When even fertile collections, many of which represent undescribed species, often cannot be identified (cf., FORERO & GENTRY, 1986), identification of the sterile material on which ecological analyses must be based becomes a truly daunting task. Although all species included in the ecological samples described here are vouchered with collections at COL and MO, many sterile collections are identified only to family or genus and the number of species in such families as Annonaceae, Sapotaceae, Lauraceae, Myrtaceae, or Guttiferae, that are represented in a given sample are based on sorting the collections by "morphospecies". Usually decisions as to which collections are conspecific are fairly straightforward within a given site but less so between sites. Moreover, even in taxa for which specific determinations are available, identification problems are sometimes encountered. For example both *Brosimum utile* ssp. *occidentale* C. Berg and *B. utile* ssp. *magdalenense* C. Berg were included in the Tutunendó sample. Since these two morphologically distinct taxa co-occur sympatrically, I have treated them as two different species, contrary to their treatment by the relevant taxonomic specialist. In a few cases I have been unable to decide whether two different collections represent the same species and in a very few cases critical vouchers failed to arrive at MO; in such cases the potential range in variation in number of species in a particular family or category is recorded in the Tables as well as in the discussion below.

At the familial level the two Chocó area pluvial forests are remarkably similar in floristic composition despite their very different soil types and low specific overlap (Table 4). Exactly the same seven families are dominant in number of species included in these samples: Leguminosae, Rubiaceae, Palmae, Annonaceae, Melastromataceae, Sapotaceae, and Guttiferae. At Bajo Calima six of these are of about equal diversity (16-18 spp.) while Annonaceae has only 12-13 species. At Tutunendó Leguminosae is clearly the most species rich

family (25 species) with Rubiaceae (17-19 spp.), Palmae (17 spp.), Annonaceae (15 spp.), Melastomataceae (14 spp.), Sapotaceae (13 spp.), and Guttiferae (12 spp.) following in that order.

The other important families in terms of species diversity are also the same for both Chocó samples. At both sites Moraceae, Lauraceae, Lecythidaceae, Myristicaceae, Euphorbiaceae, Chrysobalanaceae, and Myrtaceae are the seven next most important families with between 6 and 11 species each. While there is minor shuffling of the number of species in each of these families between the two sites the overall similarity of familial composition seems truly remarkable.

The less speciose families are also remarkably similarly represented in the two Chocó samples. Forty-six of the 56 families represented at Tutunendó are also represented at Bajo Calima and all but two (Araliaceae and Convolvulaceae, each with 2 species) of the families not also represented at Bajo Calima are represented in the Tutunendó sample by only a single species. Similarly 46 of the 60 families at Bajo Calima are present at Tutunendó and only one family (Dichapetalaceae with two species) not occurring also at Tutunendó has more than a single sampled species. Not a single family with three or more species represented at either site is missing from the second site's sample. The intersite differences in familial composition seem mostly due to random "noise" associated with the presence or absence of individual species in the samples.

Comparisons of intersite similarities in species are more difficult since specific identifications are highly incomplete and matching of "morphospecies" between sites can be done with much less confidence than within a site. Nevertheless the general pattern is clear: Despite their climatic similarities and geographic proximity there is almost no specific overlap between the two sites. Only 21 species can be confidently assigned to both sites either on the basis of specific identification or distinctive and unmistakable morphospecies. While some additional species in large taxonomically difficult groups may be shared, almost certainly fewer than 40 of the 250 species of either sample will ultimately prove to be shared with the other site. Presumably the very different soils of the two sites are largely responsible for their completely different suites of species, despite the similar familial representation. The pattern of similar familial composition of plant communities on different substrates despite very different specific compositions is exactly the same one that predominates in Amazonia (GENTRY, 1985, 1986b).

Floristic similarities with Amazonia are also pronounced in the understory. The same three families —Rubiaceae, Araceae, and Piperaceae, are the predominant fertile understory elements in both those cis-Andean and trans-

Andean forests that have average to rich soils and lack a pronounced dry season. In both regions Melastomataceae are fourth in number of fertile understory species with about 5 fertile species per 500 m transect. In both regions, Marantaceae, Palmae, Gesneriaceae, Cyclanthaceae, Solanaceae, Acanthaceae, and Commelinaceae are among the next most prevalent families. However there are also some noticeable differences between the taxonomic composition of the Chocó area understory and that of similar Amazonian forests, possibly reflecting different biogeographic histories on opposite sides of the Andes. Zingiberaceae, Musaceae, Gramineae, and Solanaceae have noticeably fewer fertile species in our Chocó samples while Gesneriaceae, Orchidaceae, Bromeliaceae, and Acanthaceae have more. Especially noteworthy differences are in Gesneriaceae (average of 4.6 fertile species per Chocó area sample vs. 1.7 in Amazonia) and Bromeliaceae (average of 1.6 fertile species per Chocó area sample vs. none encountered in Amazonia).

The majority of the wet forest understory species in Chocó, as in comparable sites in Amazonia, are shrubs, and most of these belong to Rubiaceae (av. 8.4 fertile species per transect), Melastomataceae (av. 4.6 spp.), Piperaceae (av. 5 spp.), and Solanaceae (av. 1.2 spp.). There are also a number of understory-specialized epiphytes among which Araceae predominate, but also including a few orchids, gesneriads, cyclanths, Peperomias, and bromeliads. Commelinaceae, Gesneriaceae, and Acanthaceae predominate among the wet forest terrestrial herbs, and Marantaceae, Palmae, Musaceae, Zingiberaceae, and terrestrial Araceae are predominant fertile "palmetto" elements (GENTRY & EMMONS, 1986).

While the familial composition of the two Chocó area sites is in many respects similar to that of most other Neotropical sites, there are also some noteworthy differences. Most unusual is the preponderance of species of Guttiferae and Melastomataceae in the Chocó pluvial forest samples. Both the Bajo Calima and Tutunendó samples include more species of both these families than does any other site in the world. The importance of these two families, which are rich in hemiepiphytes, is largely a result of the prevalence of hemiepiphytic climbers in Chocó plant communities (cf. above). Other families represented by hemiepiphytes in both sites include Gesneriaceae, Cyclanthaceae, Araceae, Marcgraviaceae, and Ericaceae, all families that typically enter these samples in middle elevation cloud forest but only sporadically in other lowland sites.

Some exclusively tree families like Myrtaceae and Bombacaceae are also unusually well represented in the pluvial forest plant communities. Myrtaceae are very speciose in both Chocó samples. The 10 Myrtaceae species at Bajo Calima qualify it as one of the most Myrtaceae-rich 0.1 ha. samples in the

world analyzed to date, a distinction shared with the same Semengoh Forest, Sarawak, sample that is the runner up worldwide to the Chocó samples in species diversity. However, coastal Brazil is even more species rich in Myrtaceae (cf. MORI ET AL., 1983); although the data from my single 0.1 ha. sample in Espirito Santo have not yet been tabulated, at least 25 Myrtaceae species are included.

Unusual prevalence of Bombacaceae, especially of the genus *Quararibea,* may be a generally characteristic feature of Chocó area wet forests. Not only do the Tutunendó and Bajo Calima samples include, respectively, 5 and 6-7 species of Bombacaceae but so do the sites in Ecuadorian Chocó (5-6 spp. at Centinela, 3 at río Palenque). All of the sampled Bombacaceae species, both in coastal Colombia and Ecuador, belong to *Quararibea* (or its dubious segregate *Phragmotheca*), and the trans-Andean wet forests seem to be the center of diversity for this genus, as well as the place where it attains its greatest ecological importance. At only one other site, an Ecuadorian dry forest, also in the trans-Andean region, were more than three Bombacaceae species included in these samples. The extreme in *Quararibea* prevalence may be río Palenque, Ecuador, where the second and third commonest tree species are both *Quararibea* and Centinela, Ecuador, where its five (possibly 6) sampled species make it the only genus in that sample with more than three species.

There are also more palm species in the two Chocó pluvial forest samples than in any other in the world. The Bajo Calima sample includes 17 palm species, the Tutunendó one 15. The Pipeline Road, Panamá, and Centinela, Ecuador, samples are distant runnerups with 10 and 8-9 palm species, respectively. The exceedingly high diversity (and density) of woody hemiepiphytes and palms gives the Chocó forest much of its characteristic aspect.

Another interesting feature of the Chocó pluvial forests is that plant families that are usually restricted to the Andean uplands occur at or near sea level. While these taxa rarely achieve the ecological importance they have at higher altitudes, their mere presence at such low altitudes is noteworthy. Examples from the 0.1 ha. samples include *Hedyosmum* (Chloranthaceae), *Ilex* (Aquifoliaceae), *Panopsis* (Proteaceae), *Meliosma* (Sabiaceae), and *Talauma* (Magnoliaceae). Elsewhere in the Chocó region the presence of Podocarpus on Gorgona Island (Fernández-Pérez, pers. comm.; C. Barbosa, pers. comm.) and probably elsewhere, and of the only known lowland species of Brunelliaceae, *Brunellia gentryi* Cuatr. in Chocó Department and *B. hygrothermica* Cuatr. in Valle Department, are even more extraordinary. In general the floristic difference between lowland and montane forests seems much less clearly demarcated on the Pacific than the Amazonian side of the Andes.

The poor representation of some families as compared to other neotropical lowland sites is also noteworthy, especially at Bajo Calima. For example, Bignoniaceae, usually the main neotropical liana family, is especially poorly represented in the Chocó pluvial forests (as well as in the Ecuadorian Chocó). Generally the iron and aluminum rich lateritic soil of the Tutunendó area supports a much more typical forest floristically than does the phosphorous-lacking white clay at Bajo Calima. For a wide range of similar samples from throughout much of lowland tropical America Leguminosae is almost always the most species rich family just as it is at Tutunendó. At least seven of the 11 next most species rich families are the same in all inner tropical wet and moist forest sites (GENTRY, 1985). These 11 most dominant families (after Leguminosae) are Lauraceae, Annonaceae, Moraceae, Sapotaceae, Rubiaceae, Palmae, Myristicaceae, Euphorbiaceae, Meliaceae, and Bignoniaceae. At Tutunendó, almost exactly these same families are important. Leguminosae is the most species rich family with 25 species $\geqq$ 2.5 cm dbh. in 0.1 ha. Rubiaceae, Palmae, Annonaceae, Sapotaceae, Moraceae, Lauraceae, Myristicaceae, and Euphorbiaceae are all included in the 10 most species rich families just as they are at other lowland moist and wet forest sites in Amazonia and southern Central America. Of the usual predominant families, only Meliaceae and Bignoniaceae are under-represented at Tutunendó.

The Bajo Calima site, despite the many floristic similarities to the Tutunendó one discussed above, has a less typical composition at the familial level, when compared to other neotropical lowland sites. This peculiarity is shared with both wet forest sites from the Ecuadorian Chocó, even though their familial compositions are very different (cf. Table 4). Bajo Calima is one of only three lowland continental neotropical sites where Leguminosae is not the most species rich family in this kind of sample. In the Bajo Calima sample there are only 17 species of Leguminosae (and Palmae) but ca. 19 of Rubiaceae. Interestingly, the two other lowland neotropical sites where Leguminosae is not the most species rich family are precisely the two wet forest sites from the Ecuadorian Chocó. At both Centinela and río Palenque Moraceae is the most species rich family. In both río Palenque samples Leguminosae is second in diversity only to Moraceae, but in the Centinela one it is also exceeded in number of species by Lauraceae, Palmae, and Rubiaceae, as well. Curiously, the Bajo Calima sample is notably poor in Moraceae, being one of the very few neotropical wet or moist forest samples where Moraceae is not even one of the ten most speciose families. Conversely, the Bajo Calima sample has unusually strong representation of species of Sapotaceae, Annonaceae, Lecythidaceae, and Chrysobalanaceae while these families are noticeably underrepresented at both río Palenque and Centinela. I conclude from these patterns (as well as similar data from a series of Amazonian sites: GENTRY,

1985, 1986a) that families like Moraceae specialize on rich soils while families like Leguminosae, Sapotaceae, Annonaceae, Lecythidaceae, and Chrysobalanaceae do better on poorer soils. Despite its complete dearth of phosphorus, the Bajo Calima site, both floristically and in terms of its understory fertility (and putatively productivity), is floristically more like lateritic soil sites such as Tutunendo than like the forests on extremely poor white sand soils that are prevalent in much of Amazonia. On the ultra poor white sand soils (cf. Cerro Neblina and Mishana in Table 4) even families like Sapotaceae, Lecythidaceae, and Chrysobalanaceae drop out and only Leguminosae remains species rich, the latter thus becoming truly dominant.

OTHER NOTEWORTHY FEATURES

Another peculiarity of both Chocó samples is that they have an unusually high prevalence of bird and mammal-dispersed fruits (cf. GENTRY, 1982b, 1983). Even in normally wind-dispersed families like Bignoniaceae and Bombacaceae all or most of the taxa represented in our pluvial forest sample are zoochorous. Only eight species in the entire Bajo Calima sample and 14 in the Tutunendó one appear to be primarily wind-dispersed. Excluding 7 autochorous species at Bajo Calima and seven at Tutunendó (plus a couple of probably primarily water-dispersed species), the other 235 to 250 species in each sample are apparently dispersed by birds or mammals. Thus well over 90% of the species in both of these samples are zoochorous; the ca. 94% zoochorous species at Bajo Calima is the highest such value of any site surveyed. At both sites just under half of the zoochorous species appear to be primarily mammal-dispersed and just over half bird-dispersed. The dispersal of relatively large seeds that is made possible by zoochory would appear to have an extremely strong selective advantage in the highly leached nutrient poor soils of the lowland Chocó.

Large seeds are generally characteristic of mammal-dispersal as compared to bird-dispersal (cf., GENTRY, 1982b; JANSON, 1983). The unusually high frequency of mammal-dispersal as compared to bird-dispersal in the Chocó pluvial forests may relate to this difference. Indeed several families or genera have the largest-seeded species of their respective taxa in the Chocó region. *Orbignya cuatrecasana* Dugand is possibly exceeded in fruit size among palms only by the coconut (*Cocos*) and double coconut (*Lodoicea*). *Saccoglottis ovicarpa* Cuatr. may be the largest-fruited Humiriaceae. Two of the endemic Chocó species of *Compsoneura* (Myristicaceae) encountered in our samples have the largest fruits in their genus as do two of the species of *Iryanthera* (also Myristicaceae).

There are also many apparent familial "world records" for leaf size in the Chocó pluvial forests, especially at the Bajo Calima site where both large size and extreme sclerophylly characterize the leaves of many unrelated species. Bajo Calima species with putatively the largest leaves known in the entire world for their families include *Schlegelia dressleri* A. GENTRY (Bignoniaceae), *Psittacanthus* sp. nov. (Kuijt, ined.: leaves 50-100 cm long) (Loranthaceae), *Licania gentryi* Prance (ined.) (Chrysobalanaceae), *Iryanthera megistophylla* A. C. Smith (Myristicaceae), *Ilex* sp. nov. (leaves 15-25 x ca. 10 cm) (Aquifoliaceae), and possibly *Protium amplum* Cuatr. (Burseraceae) and *Macrolobium archeri* Cowan (Leguminosae). Many other taxa apparently have the largest leaves of their respective genera. And all of the unusually large-leaved species of these sites (and the region) have unusually sclerophyllous leaves as well. Some of these large-leaved taxa range north to eastern Panamá (*Schlegelia dressleri*) or south to the Ecuadorian Chocó (*Guarea cartaguenya* Cuatr., perhaps the Meliaceae with the largest leaflets in the world) but most of the them seem to be narrow endemics in the unusual phosphorus-lacking white clay of the Bajo Calima region.

CONCLUSIONS

The Chocó area pluvial forests are characterized, both physiognomically and floristically, by a number of distinctive and for the most part previously unnoted features. Physiognomically they have unusually high densities of both small (2.5-10 cm dbh.) and medium-sized ($\geq$ 10 cm dbh.) trees, replacement of much of the normal neotropical forest component of free-climbing lianas by hemiepiphytic climbers, and many species with unusually large fruits and some of the largest and most coriaceous leaves in the world. At the community level they are characterized by the highest floristic diversity in the world, at least at the scale of 0.1 ha. samples of plants $\geq$ 2.5 cm diameter. Even on poor soils, the understory of Chocó area forests is rich and varied with a higher diversity and density of fertile understory species than most other Neotropical forests. While they share many floristic features with other neotropical lowland sites, the Chocó area pluvial forests also tend to have some unusual taxonomic makeups including generally less dominance of Leguminosae than in other parts of the lowland Neotropics, unusual prevalence of families like Guttiferae, Palmae, Myrtaceae, and Melastomataceae, and prevalence on good soils of Moraceae. Zoochory and especially mammal-dispersal are the predominant dispersal modes and some mammal-dispersed genera like *Quararibea* and *Compsoneura* have achieved a level of success both in evolutionary radiation and as ecological dominants unequalled elsewhere. Many of these features would seem more characteristic of cloud forest than

of lowland forest and may be due, like the unusual presence near sea level of typical Andean upland taxa, to the region's ever-wet cloud forest like environment.

The available evidence, while very preliminary, strongly suggests that the Chocó is not only one of the most strongly differentiated regions of the Neotropics phytogeographycally, but that it has both the perhaps most diverse plant communities in the world and extremely high levels of local as well as regional endemism. I suspect that there may be more yet-to-be-discovered plant species in the Chocó region than anywhere else in the world. Thus from the global viewpoint a major focus both on floristic inventory and conservation of this unique region would seem very much in order.

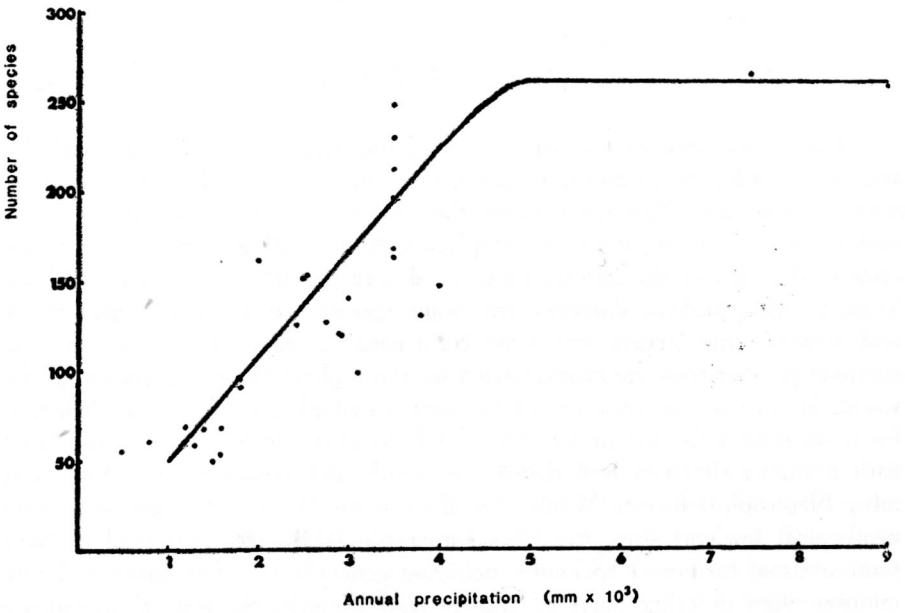

TABLE 1

Number of species and individuals in 1000 m^2 samples of lowland moist and wet forest from countries adjacent to Colombia.

Site	*No. of Families*	*Number of Species*				*Number of Individuals*				
		Total No. Spp.	*No. liana Spp.*	*No. Trees*	*No. Trees ≧ 10 cm dbh. (+ lianas)*	*Total*	*Lianas*	*Trees*	*Trees ≧ 10 cm dbh. (+ lianas)*	*Palmettos*
Curundu, Pan.	42	90	24	64	30	286	59	225	52	2
Madden F., Pan.	46(+)	126	31	93	34(+2)	324	76	242	38(+2)	6
Pipeline Rd, Pan.	59	167	38(inc. 1 hemi)	129	35(+2)	393	67(inc. 2 hemi)	325	60(+2)	1
Corcovado, C.R.	46	ca.130	34(inc. 5 hemi)	ca.96	44(+4)	291	54(inc. 7 hemi)	237	82(+4)	—
Río Palenque Ecu.	51	119	27(inc. 11 hemi)	89	25(+2)	305	63(inc. 22 hemi)	221	42(+2)	21
Río Palenque Ecu. (No. 2)	43	119	22(inc. 8 hemi)	95	32	324	45(inc. 15 hemi)	269	52	10
Jauneche, Ecu.	38	96	44(inc. 1 hemi)	52	30(+1)	435	123(inc. 1 hemi)	312	63(+1)	—
Centinela, Ecu.	55	ca.140	32(inc. 8 hemi)	106	47	419	70(inc. 13 hemi; + 1 stran.)	347	93	2

Site	*No. of Families*	*Number of Species*				*Nmber of Individuals*				
		Total No. Spp.	*No. liana Spp.*	*No. Trees*	*No. Trees ≧ 10 cm dbh. (+ lianas)*	*Total*	*Lianas*	*Trees*	*Trees ≧ 10 cm dbh. (+ lianas)*	*Palmettos*
Bosque v. Humboldt, Peru	43	154	33 (+1 strangl.)	121	40 (+3)	438	65	373	83 (+3)	—
Mishana, white sand, Peru	46 (+)	196	29	166	52	406	59	347	59	—
Mishana, lowland, Peru	59	249	60 (inc. 5 hemi)	189	68	483	86 (inc. 7 hemi)	ca.396	83	1
Mishana, tahuampa, Peru	40 (+)	168	44 (inc. 3 stran.)	124	53	514	99	415	70	—
Cocha Cashu, Peru	49	162	43	119	57 (+2)	359	79	280	77 (+2)	—
Yanamono, Peru (No. 1)	48 (+)	212	42 (inc. 2 hemi)	170	48 (+2)	303	60 (inc. 2 hemi)	242	55 (+2)	1
Yanamono, Peru (No. 2)	50 (+)	230 (—)	42 (inc. 2 hemi)	188	52 (+6)	338	57 (inc. 2 hemi; + 1 Ficus)	280	58 (+5)	—
Yanamono, tahuampa, Peru,	50	163	42 (inc. 3 hemi; +2 stran.)	123	43 (+1)	359	59 (inc. 3 hemi; + 2 strangl.)	298	72 (+1)	ca.15

Site	*No. of Families*	*Number of Species*				*Nmber of Individuals*				
		Total No. Spp.	*No. liana Spp.*	*No. Trees*	*No. Trees ≧ 10 cm dbh. (+ lianas)*	*Total*	*Lianas*	*Trees*	*Trees ≧ 10 cm dbh. (+ lianas)*	*Palmettos*
Tambopata, Peru	46(+)	151	41 (inc. 1 hemi)	110	34(+3)	360	82 (inc. 1 hemi)	302	58(+3)	—
Cabeza de Mono, Peru	40(+)	147	37 (inc. 2 hemi)	110	38(+3)	423	62 (inc. 2 hemi)	361	51(+3)	—
Mocambo, Braz.	39	132	27 (inc. 2 hemi)	105	44(+4)	315	50 (inc. 2 hemi)	265	69(+7)	—
Cerro Neblina, Venez.	31	99	22	77	29(+3)	381	31	350	57(+3)	—
Average	46	152	35	116	42	373	68	304	64	—

TABLE 2

Number of species and individuals in 1000 m^2 samples of lowland pluvial forest in coastal Colombia.

Site	*No. of Families*	*Number of Species*				*Number of Individuals*				
		Total No. Spp.	*No. liana Spp.*	*No. Trees*	*No. Trees ≧ 10 cm dbh. (+ lianas)*	*Total*	*Lianas*	*Trees*	*Trees ≧ 10 cm dbh. (+ lianas)*	*Palmettos*
Tutunendo	55 (+)	258	49 (inc. 14 hemi)	208	55	523	72 (inc. 20 hemi)	367	81	3
Bajo Calima	60 (+)	265	50 (inc. 22 hemi)	ca.240	76 (+1)	497	64 (inc. 26 hemi)	433	94 (+3)	—
Average	48	262	50	224	66	510	68	400	88	—

TABLE 3

Number of species and individuals in 1000 m^2 samples of lowland dry forest from Colombia and adjacent countries.

Site	*No. of Families*	*Number of Species*				*Number of Individuals*				
		Total No. Spp.	*No. liana Spp.*	*No. Trees*	*No. Trees ≧ 10 cm dbh. (+ lianas)*	*Total*	*Lianas*	*Trees*	*Trees ≧ 10 cm dbh. (+ lianas)*	*Palmettos*
Tayrona, Col.[1]	(21)	ca.50	12-13	37	ca.23	338	98	240	70	
Galerazamba, Col.	20	55	18	36	18(+5)	252	104	138	44(+6)	
Boca de Uchire, Ven.	20(+)	69	16	53	22	259	75	184	31	
Est. Biol. de Llanos, Ven.[1]	(21)	59	10	49	24	326	56	270	44	
Blohm Ranch, Ven.	31	68	17	51	27	306	71	235	86	
Capeira, Ecu.	27	61	19	42	30(+3)	236	61	175	66(+3)	
Guanacaste, C.R. (upland)[1]	(21)	53	6	47	18	437	81	356	34	
Guanacaste, C.R. (gallery)[1]	(33)	68	8	60	27	195	24	171	33	
Average	25[2]	60	13	47	24	294	71	221	51	

[1] Calculated from sample between 500 m^2 and 800 m^2.
[2] Calculated only from complete 1000 m^2 samples.

TABLE 4

Familial composition of Chocó Area 0.1 ha. samples.

Family	*Number of Species*				
	Bajo Calima	*Tutunendó*	*Centinela*	*R.P.(1)*	*R.P.(2)*
Acanthaceae	—	—	—	2	—
Actinidiaceae	—	—	1	—	—
Aquifoliaceae	1	—	—	—	—
Annonaceae	(12-) 13	15	4-5	2	2
Apocynaceae	6	4	2	—	1
Araceae	4 (-5)	3	3	3	3
Araliaceae	—	2	—	—	1
Bignoniaceae	1	2	2	4	5
Bombacaceae	6 (-7)	5	5 (-6)	3	3
Boraginaceae	1	1	1	1	—
Bromeliaceae	—	—	1	—	—
Burseraceae	4 (-5)	4	1	—	—
Capparidaceae	—	—	1	1	1
Caricaceae	—	—	1	3	2
Caryocaraceae	1	—	—	—	—
Celastraceae	—	—	1	—	—
Chloranthaceae	1	1	—	—	—
Chrysobalanaceae	6	7	1	1	1
Combretaceae	—	1	1	—	—
Compositae	—	1	1	2	2
Connaraceae	—	—	1	—	—
Convolvulaceae	—	2	—	—	—
Cucurbitaceae	—	—	1	—	—
Cyclanthaceae	2	2	2	2	1
Dichapetalaceae	2	—	—	—	—
Dilleniaceae	5	2	—	—	—
Ebenaceae	1	—	—	—	—
Elaeocarpaceae	1	3	1	—	1
Ericaceae	2	2	1	—	—
Euphorbiaceae	(5-) 6	7	2	4	3
Ferns	—	1	—	3	2
Flacourtiaceae	3	2	1	1	2
Gesneriaceae	1	1	—	—	—
Gnetaceae	1	—	—	—	—
Gramineae	—	—	—	1	1
Guttiferae	ca.16	12	4	2	2
Hernandiaceae	—	—	—	1	1
Hippocrateaceae	4	1	—	—	—
Humiriaceae	1	1	—	—	—
Icacinaceae	1	—	1	1	—
Lacistemaceae	—	—	—	1	—
Lauraceae	(10-) 11	9	8 (-11)	3	7
Lecythidaceae	7 (-9)	8	5	1	2
Leguminosae	(16-) 17	25	7	8	8
Linaceae	1	—	—	—	—

TABLE 4

Familial composition of Chocó. Area 0.1 ha. samples.

Family	*Number of Species*				
	Bajo Calima	*Tutunendó*	*Centinela*	*R.P.(1)*	*R.P.(2)*
Loganiaceae	4(-5)	3	1	—	—
Magnoliaceae	1	—	—	—	—
Malpighiaceae	1	1	1	—	1
Marantaceae	—	1	—	—	—
Marcgraviaceae	2(-3)	3	2	1	2
Melastomataceae	16(-17)	14	5-7	2	4
Meliaceae	2	4	5-7	4	6
Menispermaceae	2	2	2	3	—
Monimiaceae	2	2	1	1	—
Moraceae	7	11	9	11	12
Musaceae	—	—	2	2	2
Myristicaceae	11	7	—	4	5
Myrsinaceae	3	5	2	2	1
Myrtaceae	10-11	6	3	—	—
Nyctaginaceae	1	1	—	1	1
Ochnaceae	—	1	—	—	—
Olacaceae	1	1	1	1	1
Palmae	17	17	8-9	6	6
Passifloraceae	1	3	1	—	—
Phytolaccaceae	—	—	—	1	—
Piperaceae	—	—	3	5	5
Polygalaceae	—	1	1	—	—
Polygonaceae	1	—	2	1	—
Proteaceae	1	—	—	—	—
Quiinaceae	1	—	—	—	—
Rhizophoraceae	1	—	—	—	—
Rubiaceae	ca.19	17-19	8	7	4
Rutaceae	1	—	—	1	—
Sabiaceae	1	1	—	1	1
Sapindaceae	1	5-7	3	1	4
Sapotaceae	ca.17	13	1	1	2
Saxifragaceae	—	—	1	—	—
Simaroubaceae	2	1	—	1	1
Solanaceae	—	—	2	4	5
Sterculiaceae	1	1	1	1	1
Thymelaeaceae	—	1	1	1	1
Tiliaceae	—	1	—	—	—
Ulmaceae	—	—	—	1	2
Urticaceae	—	—	1	1	—
Verbenaceae	1	1	—	2	2
Violaceae	1	2	1	—	—
Vitaceae	—	—	2	—	—
Vochysiaceae	3(-4)	1	1?	—	—
Zingiberaceae	—	—	—	1	—
Indets.	3	2	—	—	—